OCCURRENCE AND TIMING OF EGG TEETH IN BIRDS

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The egg tooth is a small tooth-like protuberance on the distal end of the dorsal surface of the upper mandible at the time of hatching. It is generally believed that the egg tooth functions in cutting through the shell membranes and shell at hatching. In addition to egg teeth on the upper mandible, a number of authors have noted tooth-like modifications of various kinds at the tip of the lower mandible in embryos or newly hatched birds of a variety of families. The objective of this paper is to present an extended review of scattered records of egg teeth as a stimulus and aid for further studies on the morphology, function, development, and evolution of these structures.

In spite of the great significance of hatching in the life of the bird, very little is known of the causal relations involved in the process. Certain correlated events such as respiratory, circulatory, and behavioral changes are known, but in no case have the factors responsible for the timing of hatching been specifically identified. The role of the egg tooth in hatching also needs further study. Fisher (1958) studied the development in the chicken of the hatching muscle which may be important in the functioning of the egg tooth. It has been suggested that the hatching muscle provides a major part of the thrust in breaking through the shell. The egg tooth is possibly unique as a structure functional only at the time of hatching. Many species appear to have characteristic patterns of hatching as shown by the condition of the shells after hatching (Wetherbee, 1959). In the European Quail (*Coturnix coturnix*), for example, the blunt end of the shell is almost entirely cut off with a precise circular incision.

The egg tooth of the upper mandible has been studied in detail for only a very few species. A modern histological study of the egg tooth is that of Kingsbury, Allen, and Rotheram (1953) on the chicken. Detailed comparative studies are needed to determine the homologies of the egg teeth of both upper and lower mandibles within the class Aves. In some groups (e.g., penguins and Falconiformes) the egg tooth of the upper mandible typically remains visible for several weeks posthatching, while in other forms (e.g., many Galliformes) loss of the egg tooth characteristically occurs within a few days posthatching (Table 1). Gardiner (1884) suggested that there is a tendency for nidicolous species to retain the egg tooth longer than do nidifugous ones. The physiological and environmental factors involved in retention or disappearance of egg teeth are virtually unstudied.

Gadow (1891) and others have stated that the egg tooth in birds was first noted by Yarrell (1826), but Anson (1929) reported two earlier observations: Aldrovandi in 1600 and Hunter in 1793 (the latter report not published until 1841). Gadow (1891) stated that the egg tooth is to be found in the embryos of

TABLE 1

TIME OF DISAPPEARANCE OF THE EGG TOOTH IN VARIOUS BIRDS

A. The egg tooth is reduced or disappears before hatching:
   some Megapodiidae
B. The egg tooth disappears during the first week posthatching:
   Hydrobates pelagicus (Hydrobatidae)
   Eudocimus albus (Threskiornithidae)
   some Anatidae
   some Galliformes
   Rallus elegans (Rallidae)
   some Scolopacidae
   some Passeriformes
C. The egg tooth disappears after the first week posthatching:
   some Spheniscidae
   Procellaria grisea (Procellaridae)
   some Falconiformes
   some Otididae
   Cepphus grylle (Alcidae)
   Turacus hartlaubi (Musophagidae)
   Tyto alba (Tytonidae)

all birds, but evidence for this opinion was not presented. The data here compiled support Gadow's claim, but the chance of finding species without egg teeth remains. It appears that in most branches of avian phylogeny the egg tooth has been developed or retained as an integral part of the hatching process.

Failure of an observer to find an egg tooth on a newly hatched bird does not necessarily indicate that an egg tooth is absent in that species; absence of an egg tooth in a particular specimen may be an age variation rather than a species-specific character. Within a species there may well be wide variation in the time of disappearance of the egg tooth; precise data are needed on this point.

In reptiles at least two types of egg teeth are known: one a true dentinal structure and the other of integumental origin. Only the latter type of egg tooth is known from birds. Some authors have restricted the term "egg tooth" (*Eizahn*) to egg teeth of dentinal character; such terms as egg callosity (*Eischiele*), "egg caruncle," "shell breaker." or "pipping tooth" are used for the structure found in birds. However, the term "egg tooth" is so widely used for the avian integumental derivative that there seems little to be gained by a change of terminology.

No attempt has been made in this paper to review all the published records of egg teeth. A primary concern has been to find records for as many of the major groups of birds as possible. Many records undoubtedly have been missed. In addition to checking several hundred published articles and books, I have

examined study skins and alcoholic specimens at the Yale Peabody Museum of Natural History. Examination of specimens at other large museums would unquestionably yield many additional records of egg teeth.

SYSTEMATIC ACCOUNT

Spheniscidae.—The egg tooth is known for the following species: *Aptenodytes forsteri* (Pycraft, 1907*a*), *Pygoscelis papua* (Murphy, 1936), *P. antarctica* (Parsons, 1932), *Eudyptes chrysocome* (= *E. crestatus*; Lewin, 1903), and *Eudyptula minor* (Grossenheider, 1952).

Struthionidae.—Röse (1892) and Schneider (1949) reported and figured the egg tooth of *Struthio camelus*. Schneider's figures of the newly hatched bird suggest the presence of a well-developed hatching muscle.

Gaviidae.—A study skin of a downy *Gavia immer* bears an egg tooth on the tip of the upper mandible. Stresemann (1927–34) commented that newly hatched loons have a tooth-like callosity on the tip of the lower mandible.

Podicipedidae.—Egg teeth were found on downy study skins of *Colymbus chilensis* and *Aechmophorus occidentalis*. Simmons (1955) observed an egg tooth on the distal quarter of the upper mandible of a downy *Colymbus* (= *Podiceps*) *cristatus*.

Procellariidae.—The white egg tooth of the chick of *Procellaria grisea* disappears between 11 and 22 days posthatching with 17½ days being the average time (Richdale, 1945).

Hydrobatidae.—Davis (1957) noted that in *Hydrobates pelagicus* the white egg tooth is retained to about six days posthatching.

Pelecanoididae.—A prominent white egg tooth on a chick of *Pelecanoides urinatrix* of an estimated age of two days posthatching was observed by Richdale (1943).

Phalacrocoracidae.—Lewis (1929) found that the egg tooth of the upper mandible of *Phalacrocorax auritus* is lost about four days posthatching. The whitish tip of the lower mandible has the appearance of an egg tooth and is retained much longer than the egg tooth of the upper mandible. Boetticher (1928) figured the egg tooth of *P. carbo*.

Ardeidae.—Sushkin (1912) reported and figured the egg tooth of *Ardea cinerea*. Heilmann (1927) also figured the egg tooth of *Ardea*.

Threskiornithidae.—Beebe (1914) reported that the egg tooth of *Guara alba* (= *Eudocimus albus*) is lost about the third day posthatching.

Anatidae.—Yarrell (1826) noted the egg tooth in ducks and geese, especially *Alopochen aegyptiacus*. Heilmann figured the egg tooth of *Somateria*. According to Romanoff (1960), *Anas platyrhynchos*, *Anser anser*, *Cygnus*, and *Mergus* lose the egg tooth a few hours after hatching. Koeche (1958) mentioned the egg tooth in his study of the embryology of *Anas platyrhynchos*. I have observed the egg tooth on the nail of the bill in downy specimens of *Aythya valisineria*, *Netta rufina*, and *Clangula hyemalis*.

Accipitridae.—A prominent white egg tooth present at hatching was lost by three weeks posthatching in *Elanus caeruleus* (Van Someren, 1956). Haverschmidt (1959) found a white egg tooth on a nestling of *Helicolestes hamatus*. Gardiner (1884) figured a tooth-like papilla on the tip of the lower mandible of an embryo of *Milvus milvus*. In *Astur* (= *Accipiter*) *tachiro* a white egg tooth was still present at 12 days posthatching (Van Someren, 1956). Van Someren (1956) found an egg tooth on *Meliërax gabar* at least two and one-half weeks posthatching. In *Aquila chrysaëtos* the egg tooth is very noticeable at hatching (Sumner, 1929). As the bill grows, the egg tooth becomes less and less noticeable; at four weeks posthatching the egg tooth is still visible, though very small. Herrick (1932) reported that the egg tooth persists for over a month posthatching in *Haliaeetus leucocephalus*. I have seen an egg tooth in a downy specimen of *Buteo jamaicensis*.

Pandionidae.—P. L. Ames (pers. comm.) found that the egg tooth remained visible in one young Osprey for at least 28 days posthatching.

Megapodiidae.—A vestigial egg tooth in embryos of *Talegalla jobiensis* and *Leipoa ocellata* has been interpreted as one of several characters indicating that megapodes have evolved from gallinaceous birds which hatched relatively earlier in ontogeny (Clark, 1960, and MS). Friedmann (1931) found no egg tooth in an embryo of *Megapodius pritchardii* shortly prehatching; presumably a vestigial egg tooth could be found earlier in the ontogeny of this species. Megapodes are reported to hatch by kicking their way out of the shell (Clark, 1960).

Phasianidae.—Stoddard (1931) noted an egg tooth on a downy *Colinus virginianus*. The development of the egg tooth in *Coturnix coturnix* has been figured by Padgett and Ivey (1960) and Romanoff (1960; after Weber). In this species the egg tooth is lost by the second day posthatching (Clark, MS). A downy specimen of *Gallus gallus* shows an egg tooth. The egg tooth on the upper mandible first becomes apparent in *Gallus domesticus* embryos at seven days of incubation (Hamilton, 1952; Kingsbury et al., 1953). According to Friedmann (1955), Rosenstadt reported an egg tooth anlage on the lower jaw of the chicken embryo. Yarrell (1826) observed that the chicken has lost the egg tooth of the upper mandible by two to three days posthatching. Friedmann (1955:21) erroneously stated that in *Gallus* embryos the egg tooth of the upper mandible is already present at the time of an oral invagination separating upper and lower jaws. Using the figures of Gardiner (1884), Friedmann misidentified the labial groove by calling it an oral invagination; Hamilton (1952:374–375) has given this correct interpretation of Gardiner's study. In embryos of *Phasianus colchicus* the egg tooth is quite noticeable as early as the ninth day of incubation (Fant, 1957). The egg tooth of the Ring-necked Pheasant remains for one or two days posthatching, rarely longer; sometimes the egg tooth is lost as early as five to six hours after hatching (Westerskov, 1957).

Opisthocomidae.—Beddard (1889) and Parsons (1954) noted the egg tooth in *Opisthocomus*.

Gruidae.—Egg teeth have been observed in newly hatched *Grus americana* (Allen, 1952) and *G. canadensis* (Walkinshaw, 1950).

Psophiidae.—Burckhardt (1901*b*) reported an egg tooth for *Psophia crepitans*.

Rallidae.—The egg tooth is lost in *Rallus elegans* between the fourth and sixth days posthatching (Meanley and Meanley, 1958). Walkinshaw (1937) observed the egg tooth in *Rallus limicola*. *Gallinula chloropus* is stated to have a tooth-like callosity on lower mandible (Willink, 1899). Steinmetz (1932) noted the egg tooth of *Fulica atra* (Heilmann, 1927, also figured the egg tooth of *Fulica*). Falla (1951) reported an egg tooth in *Notornis*.

Rhynochetidae.—Burckhardt (1901*a*) noted the egg tooth in *Rhinochetos jubatus*.

Otididae.—Romanoff (1960) commented that bustards retain the egg tooth for several weeks posthatching. Willink (1899) found a tooth-like callosity on the tip of the lower mandible of *Otis afra* (= *Afrotis atra*); Willink also noted an egg tooth on the upper mandible.

Haematopodidae.—Among the variety of species with a tooth-like callosity on the lower jaw is *Haematopus ostralegus* (Willink, 1899).

Charadriidae.—Romanoff (1960; after Rezovska) has reported a small egg tooth on the anterior end of the lower mandible of *Vanellus vanellus*.

Scolopacidae.—Willink (1899) found an egg tooth on the anterior end of the lower jaw of *Numenius* and *Limosa aegocephala* (= *L. limosa*). Romanoff (1960) reported that in *Gallinago* (= *Capella*) *gallinago* and *Scolopax rusticola* the egg tooth of the upper mandible

is lost a few hours after hatching. Wetherbee (1959) was unable to find an egg tooth in a newly hatched *Philohela minor*.

Recurvirostridae.—Willink (1899) observed an egg tooth on the lower mandible of *Recurvirostra avosetta*.

Burhinidae.—*Oedicnemus crepitans* (= *Burhinus oedicnemus*) has an egg tooth on the lower jaw (Willink, 1899).

Laridae.—Tinbergen (1953) commented on the egg tooth in *Larus argentatus* and showed that typically the initial pipping of the shell is directed vertically, either upward or downward. Kirkman (1931) found that the egg tooth is used in hatching in *Larus ridibundus*. Röse (1892) figured the egg tooth on the upper jaw of *Sterna wilsoni* (= *Chlidonias hybrida*). Willink (1899) found an egg tooth on the lower jaw of *Chlidonias nigra*.

Alcidae.—Winn (1950) observed that in *Cepphus grylle* the egg tooth becomes relatively smaller following hatching; the egg tooth disappears between the 25th and 35th day posthatching. Lockley (1953) figured the egg tooth of the Puffin, *Fratercula arctica*.

Columbidae.—Yarrell (1826) and Wetherbee (1959) have noted the typical egg tooth on the upper mandible of *Columba livia*. The egg tooth on the upper mandible of *Zenaidura macroura* is lost about seven to eight days posthatching (Hanson and Kossack, 1957). Both Hanson and Kossack (1957) and Wetherbee (1959) commented on the egg tooth of the lower mandible of the Mourning Dove; Hanson and Kossack noted that the egg tooth of the lower mandible is still prominent at nine days posthatching. Egg teeth have been reported on both upper and lower mandibles in the following species: *Geopelia cuneata*, *Columbina picui*, *Phaps elegans*, *Geophaps scripta*, *Leptotila rufaxilla*, and *Oreopeleia montana* (Minchin, 1933; Newman, 1908). Newman (1908) thought that *Columba* and *Turtur* lack egg teeth on the lower jaw. The egg tooth on the upper mandible of *Phlogaenas crinigera* (= *Gallicolumba criniger*) was reported by Newman (1909).

Psittacidae.—Pycraft (1907*b*) noted an egg tooth on the upper mandible of a nestling *Calopsittacus novae-hollandiae* (= *Nymphicus hollandicus*). Gardiner (1884) reported an egg tooth on the upper mandible of *Melopsittacus*.

Musophagidae.—In *Turacus hartlaubi* the egg tooth disappears about ten days posthatching (Van Someren, 1956). Moreau (1938) found a very small whitish egg tooth on the upper jaw of a newly hatched chick of *Corythaeola cristata*.

Cuculidae.—Shelford (1900) reported and figured an egg tooth in embryos of *Centropus sinensis*. A relatively small egg tooth is to be found on the upper mandible of *Crotophaga sulcirostris* (Skutch, 1959).

Tytonidae.—Pickwell (1948) noted an egg tooth on *Tyto alba* at 13 days posthatching.

Strigidae.—Heilmann (1927) figured the egg tooth of *Nyctea*.

Trogonidae.—The egg tooth has been noted in *Pharomachrus mocino* (Skutch, 1947).

Bucerotidae.—Shelford (1899) examined a late embryonic stage of *Buceros rhinoceros* and noted that the sharp edge of the extreme tip of the large upper mandible could act as an egg tooth, although no actual egg tooth was observed. On the anterior end of the projecting lower mandible is a small tooth-like papilla.

Capitonidae.—Skutch (1944) commented that egg teeth of nestlings of *Dicrorhynchus* (= *Semnornis*) *frantzii* are less prominent than those of woodpeckers (Picidae). Friedmann (1955) noted a tooth-like protuberance on the upper mandible of a nestling *Megalaima asiatica*.

Indicatoridae.—Ranger (1955) reported an egg tooth at the base of the premaxillary hook in a nestling of *Indicator minor*; Friedmann (1955) suggested that the hooks of both upper and lower mandibles of nestling *Indicator indicator* are formed from anlagen homologous to those forming the egg teeth in other birds.

Ramphastidae.—Van Tyne (1929) observed a well-developed egg tooth in young *Ramphastos sulfuratus* (= *R. brevicarinatus*).

Picidae.—In *Colaptes auratus* Wetherbee (1959) found a white covering on the tips of both jaws; this covering resembled egg teeth in color and texture. Friedmann (1955) observed an egg tooth in each of two nestling specimens of *Colaptes auratus*. Lüdicke (1933) found an anlage of an egg tooth in an embryo of *Picus viridis* at five days of incubation. According to Wetherbee (1959), the Heinroths figured a nestling *Picus viridis* showing the whitish tips of both mandibles. According to Friedmann (1955), the Heinroths also reported an egg tooth on the upper jaw of *Dryocopus martius*. Hoyt (1944) described the whitish tips of each jaw of the nestling *Dryocopus pileatus*; these tips are retained until shortly after the young bird leaves the nest. Hoyt was uncertain whether these whitish tips are forms of egg teeth or whether an actual egg tooth appears earlier and is lost shortly posthatching. Egg teeth on the upper mandible of chicks of *Dendrocopos pubescens* have been reported by Friedmann (1955) and Wetherbee (1959). Friedmann (1955) found an egg tooth on a nestling *Picoïdes tridactylus*.

Corvidae.—P. L. Ames (pers. comm.) has seen an egg tooth on a nestling *Corvus brachyrhynchos*.

Troglodytidae.—Armstrong (1955) reported egg teeth in two species of wrens.

Turdidae.—Lüdicke (1933) found anlagen of egg teeth on both upper and lower jaws in embryos of *Turdus merula*.

Laniidae.—Miller (1931) noted that the egg tooth of *Lanius ludovicianus* was undiminished in size between hatching and four days posthatching. In the fifth and sixth day posthatching the egg tooth was less prominent as a consequence of growth of the remainder of the bill.

Callaeidae.—McKenzie (1951) reported that in *Callaeus cinerea* the egg tooth is retained at least one week posthatching.

Sturnidae.—Romanoff (1960; after both Portmann and Weber) has figured the egg tooth of *Sturnus vulgaris*.

Vireonidae.—Southern (1958) noted a prominent whitish egg tooth in the newly hatched Red-eyed Vireo (*Vireo olivaceus*); by the fourth day posthatching the egg tooth had decreased in size.

Icteridae.—Daniel (1957) found that the egg tooth first appears in embryos of *Agelaius phoeniceus* at the seventh day of incubation; the egg tooth is completely formed by 11½ days of incubation. Daniel also found an anlage of the egg tooth on the lower mandible of *Agelaius*. Friedmann (1929) found the egg tooth still present in *Agelaioides* (= *Molothrus*) *badius* at about five days posthatching; the following day the egg tooth was less distinct. Friedmann also observed an egg tooth in *Molothrus rufo-axillaris*. In *M. bonariensis* the egg tooth is still as prominent at three days posthatching as at hatching; the egg tooth is still present at five days posthatching but on the following day is no longer very distinct (Friedmann, 1929). In *Molothrus ater* the egg tooth is still present on the fifth day posthatching; on the sixth day it is no longer distinct. Friedmann (1929) also found an egg tooth in *Tangavius aeneus* at one day posthatching.

Tersinidae.—Traces of an egg tooth are visible in *Tersina viridis* during the first few days posthatching (Schaefer, 1953).

Ploceidae.—Lüdicke (1933) found an anlage of the egg tooth in the canary embryo at seven days of incubation; he also noted an anlage of the egg tooth on the lower jaw in this form. Weaver (1942) briefly described the egg tooth of *Passer domesticus*; this egg tooth disappears by the fourth day posthatching.

Fringillidae.—Orr (1945) observed an egg tooth in nestlings of *Geospiza*. Woolfenden (1956) recorded the egg tooth present as late as the sixth day posthatching in *Ammospiza*.

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Walt has varied interests in ornithology, but especially is he interested in the migration, life histories, and ecology of birds. He has published approximately 100 papers on these subjects and on others in allied fields of entomology, geology, and mineralogy.

Our new Life Member is also a member of the AOU, Cooper Ornithological Society, Detroit Audubon Society (Pres. 1941–1943), Michigan Audubon Society (Board Member), Massachusetts Audubon Society, National Audubon Society, numerous bird banding organizations, Michigan Botanical Club (Pres. 1947–1949), and others.